

Systematic wood anatomy of *Myodocarpus*, *Delarbrea*, and *Pseudosciadium* (Araliaceae)

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ABSTRACT

Wood anatomical features examined in five species of *Myodocarpus*, four species of *Delarbrea*, and the single member of *Pseudosciadium* (Araliaceae) using light and scanning electron microscopy support the hypotheses that they are a closely related, monophyletic group, and that they form an ancient lineage that has survived and diversified on the island of New Caledonia, where all except two of the 17 species belonging to these genera are endemic. *Delarbrea* and *Pseudosciadium* have similar wood structure; the wood of *Myodocarpus* is distinctly more primitive (sensu BAILEY). These genera differ markedly in wood structure from other Araliaceae in the presence of apotracheal (diffuse and diffuse-in-aggregates) axial parenchyma, and wood features do not support earlier suggestions that *Myodocarpus* is intermediate between Araliaceae and Apiaceae. Within *Myodocarpus* two groups of species can be distinguished on wood characters, which correspond to the species with simple vs. pinnately compound leaves. The wide-ranging *D. paradoxa* subsp. *paradoxa* is the only taxon studied with numerous vasicentric tracheids, often regarded as an adaptation to water stress.

KEY WORDS

Myodocarpus,
Delarbrea,
Pseudosciadium,
Araliaceae,
wood anatomy,
vasicentric tracheids,
phylogeny,
New Caledonia.

RÉSUMÉ

Les caractères anaromiques du bois ont été examinés pour cinq espèces de *Myodocarpus*, quatre espèces de *Delarbreia*, et l'unique espèce de *Pseudosciadium* (Araliaceae) aux microscopes photonique et électronique à balayage. Les résultats obtenus confirment que ces genres sont proches, constituent un groupe monophylétique et forment une lignée ancienne qui a survécu et s'est diversifiée en Nouvelle-Calédonie, où 15 des 17 espèces de ces genres sont endémiques. La structure du bois de *Delarbreia* et *Pseudosciadium* est semblable ; celle de *Myodocarpus* est bien plus primitive (sensu BAILEY). Ces trois genres ont une structure anatomique du bois nettement différente de celle des autres Araliaceae en raison de la présence d'un parenchyme axial apotrachéal (diffus à diffus-agrégé). L'ensemble des caractères observés n'est pas compatible avec l'idée que *Myodocarpus* occupe une position intermédiaire entre les Araliaceae et les Apiaceae. Chez les *Myodocarpus* deux groupes d'espèces peuvent être distingués par l'anatomie du bois : celles à feuilles simples et celles à feuilles composées. *Delarbreia paradoxa* subsp. *paradoxa*, à large répartition, est le seul taxon étudié à posséder de nombreuses trachéides vasocentriques, caractère souvent considéré comme une adaptation au stress hydrique.

MOTS CLÉS

Myodocarpus,
Delarbreia,
Pseudosciadium,
Araliaceae,
anatomie du bois,
trachéides vasocentriques,
phylogénie,
Nouvelle-Calédonie.

INTRODUCTION

Myodocarpus, *Delarbreia*, and *Pseudosciadium* form a closely related group of genera centred in New Caledonia (LOWRY 1986a, 1986b). All ten species of *Myodocarpus* and the single species of *Pseudosciadium* are endemic to this island, situated in the southwest Pacific. Moreover, four of the six species of *Delarbreia* are likewise restricted to New Caledonia; *D. paradoxa* Vieill. subsp. *paradoxa* also extends through Vanuatu and the Solomon Islands to the Moluccan and Lesser Sunda Islands, and *D. michiana* (F. v. Muell.) F. v. Muell., previously placed in the monotypic genus *Porospermum* F. v. Muell., is endemic to Queensland, Australia (LOWRY 1986a, 1986b).

The plants of this alliance are monocaulous or sparsely branched treelets or trees ranging from ca. 1.5 to 20 m in height, with leaves that are densely clustered at the branch ends, and whose petiole bases are clasping, as in many other Araliaceae. The three genera share a number of other characters, including similar inflorescence structure and organization, articulated pedicels, an isomerous androecium, and a bicarpellate gynoeceum, although each of these features also occurs individually elsewhere in the family. Their

floral vascularure is also relatively primitive (EYDE & TSENG 1971). However, *Myodocarpus*, *Delarbreia*, and *Pseudosciadium* differ from all other Araliaceae by the presence of distinctive secretory oil ducts in the fruits (EYDE & TSENG 1971; LOWRY 1986a, 1986b), which appear to represent a derived character (synapomorphy). Moreover, the apotracheal axial parenchyma found in the wood of the first two genera is also unknown among other members of the family (RODRIGUEZ 1957; OSKOLSKI 1994; but see below regarding *Pseudosciadium*).

Myodocarpus stands out by being the only genus of Araliaceae with a dry, laterally compressed, schizocarpic fruit with a central carpophore, whose overall morphology is at least superficially similar to the fruits of many Apiaceae (by contrast, the fruits of *Delarbreia* and *Pseudosciadium* are terete drupes). On this basis, BAUMANN (1946) regarded *Myodocarpus* as a possible link between Araliaceae and its traditional sister group, Apiaceae (see also THORNE 1973), which together are widely recognized as comprising the order Araliales. More recently, however, a number of studies have questioned such an intermediate position for the genus (RODRIGUEZ 1957, 1971; EYDE & TSENG 1971; LOWRY

1986a, 1986b; OSKOLSKI 1994; PLUNKETT 1994; PLUNKETT et al. 1996). LOWRY (1986a) points out that the fruits of all three genera share a single basic anatomical plan, with each tissue present in the fleshy fruits of *Delarbrea* and *Pseudosciadium* having a direct homologue in those of *Myodocarpus*, including the characteristic oil ducts.

The close relationship between *Delarbrea* and *Myodocarpus* was first pointed out by VIEILLARD (1865), BENTHAM (1867), and later HARMS (1894-97), HUTCHINSON (1967), and TSENG & HOO (1982) placed these genera in the tribe Aralieae Benth., whereas VIGUIER (1906) and TAKHTAJAN (1987) treated them as members of a segregate tribe Myodocarpeae (erroneously referred to as Myodocarpineae by VIGUIER). The systematic placement of *Pseudosciadium* has a somewhat more complex history. When BAILLON (1878, 1879) first described *Pseudosciadium balansae*, he indicated that it was closely related to both *Delarbrea* and *Myodocarpus*, and further suggested that it was intermediate between them. In later treatments of Araliaceae (HARMS 1894-97; VIGUIER 1906, 1925; HUTCHINSON 1967), however, *Pseudosciadium* was separated from both genera, and included in the tribe Mackinlayeae, which was rigidly (and artificially) defined by valvate, clawed petals. The close relationship of *Pseudosciadium* to *Delarbrea* and *Myodocarpus* initially suggested by BAILLON was confirmed when oil ducts were observed in the fruits of *Pseudosciadium* by LOWRY (1986a, 1986b), who concluded on the basis of this and other characters that these three genera comprise a monophyletic group. He further suggested that they represent the relicts of an ancient araliaceous lineage forming part of a floristic ensemble that was able to survive in the relatively equable climates of New Caledonia, but was in large part eliminated from Australasia and elsewhere as a result of changing climatic conditions in Neogene times (see also RAVEN & AXELROD 1972, 1974; RAVEN 1980; LOWRY in press). More recently, PLUNKETT (1994 and PLUNKETT et al. 1996), using molecular and morphological characters to examine relationships within Araliales, concluded that the available data support the hypothesis that *Delarbrea* (the only one

of the three genera under consideration here that was included in his study) is part of an ancient group from which both Araliaceae and Apiaceae evolved.

Structural features of wood offer a useful tool for improving our understanding of the systematic position of *Myodocarpus*, *Delarbrea*, and *Pseudosciadium* within Araliaceae, as well as the relationships among these three genera. Previously published data on the wood structure of these taxa are scanty, and hence insufficient to develop any conclusive interpretations. Only four species of *Myodocarpus* have been studied previously [*M. simplicifolius* Brongn. & Gris (KRIBS 1937; OSKOLSKI 1994); *M. pinnatus* Brongn. & Gris (SARLIN 1954); *M. fraxinifolius* Brongn. & Gris and *M. involucratum* Dubard & Vig. (RODRIGUEZ 1957); *Myodocarpus* sp. (RECORD & HESS 1944; METCALFE & CHALK 1950)], while only a single member of *Delarbrea* had been examined [*D. paradoxa* subsp. *paradoxa* (OSKOLSKI 1994)].

This study, which is part of a general survey of wood anatomy throughout the family (OSKOLSKI 1994, 1995, 1996; OSKOLSKI & LOWRY in prep.), examines the wood structure of a much larger sample of *Myodocarpus*, *Delarbrea*, and *Pseudosciadium*, and considers the results with regard to the systematic relationships of the group. The conclusions from such systematic analyses of wood structural features represent an important contribution to an overall understanding of the family, and will assist in preparing further revisions of Araliaceae for the Flore de la Nouvelle-Calédonie (LOWRY 1986a, 1986b, in prep.) and other regions in the Pacific (LOWRY 1987, 1988, 1989, 1990, in prep.; LOWRY et al. 1989). Moreover, this type of study provides additional morphological information for ongoing comparative phylogenetic analyses based largely on molecular data (PLUNKETT 1994; PLUNKETT et al. 1996).

MATERIALS AND METHODS

Most of the wood specimens examined were collected by the second author during field investigations

conducted in New Caledonia (voucher herbarium specimens are deposited at MO, NOU, P, and various other institutions). Some additional material was obtained from the wood collection of the Smithsonian Institution (USw), and one sample was taken from an individual growing in cultivation at the Botanical Garden of the V.L. Komarov Botanical Institute, St. Petersburg. Specimens examined in this study were mostly taken from trunks or stems with a secondary xylem radius of more than 10 mm (8 mm in *D. montana* Vieill. ex R. Vig. subsp. *arbores* (Vieill. ex R. Vig.) Lowry, and in *Delarbrea paradoxa* Vieill. subsp. *paradoxa*, and 5 mm in *D. michieana* F. v. Muell.).

Standard procedures for the study wood structure were employed to prepare sections and macerations for light microscopic studies. Specimens for scanning microscopy were prepared according to EXLEY et al. (1977). Descriptive terminology and measurements follow CARLQUIST (1988) and the I.A.W.A. List of Microscopic Features for Hardwood Identification (1989), except for the diameter of intervessel pits, for which the vertical dimension is recorded.

RESULTS

The wood anatomical data for *Myodocarpus simplicifolius* (USw W-4736) and *Delarbrea paradoxa* subsp. *paradoxa* (cult. in St. Petersburg) published earlier in Russian (OSKOLSKI 1994) are included in the following descriptions.

MYODOCARPUS (Fig. 1A-B, 2A-B, 4A-D, 5A-B,D, 6A-D, 7F-H; Table 1).

MATERIAL STUDIED.—*Myodocarpus elegans* Dubard & R. Vig. var. *gracilis* Dubard & R. Vig.: New Caledonia, Mé Ori, Lowry 3377A.—*M. fraxinifolius* Dubard & R. Vig.: New Caledonia, Rivière Bleue, Lowry 3679; sine loc., Buchholz, USw 20844.—*M. pinnatus* Brongn. & Gris: New Caledonia, Mt. Panié, Lowry 3318.—*M. simplicifolius* Brongn. & Gris: New Caledonia, Plateau de Dogny, Lowry 3216; sine loc., USw W-4736.—*M. sp. nov.*, ined.: New Caledonia, Mr. Taom, Lowry 3772.

Growth rings absent (*M. fraxinifolius* (Fig. 1A), *M. sp. nov.*, ined. (Lowry 3772)) or indistinctly marked by zones of more abundant axial parenchyma tending to form long tangential lines (*M. pinnatus*, *M. elegans*), and also of more numerous vessels (*M. simplicifolius*, Fig. 1B).

Vessels rounded, rarely angular in outline,

rather small (tangential diameter < 100 µm in *M. pinnatus*, and < 70 µm in the other species) and numerous (up to 282 per mm² in *M. elegans*); solitary mixed with few radial multiples of 2-3 (up to 7 in *M. elegans* and *M. fraxinifolius*). Vessel walls 2-6 µm thick. Tyloses not observed. Vessel elements (400-)830-1240 (-1470) µm in length. Perforation plates scalariform (Fig. 4A-C) with numerous bars (up to 20 in *M. elegans* and *M. simplicifolius*) and reticulate (Fig. 4D); rarely simple (observed in *M. fraxinifolius* only), in more or less oblique end walls. Intervessel pits alternate, opposite, and rarely scalariform (*M. elegans*, *M. sp. nov.*, ined. (Lowry 3772), Fig. 5A), 4-6 µm in vertical diameter, rounded or oval, with slit-like apertures surrounded and/or interconnected by shallow, groove-like wall sculptures (Fig. 5B,D). Vessel-ray pits similar to intervessel pits in size and shape (*M. pinnatus* (Fig. 6B), *M. fraxinifolius*) or predominantly scalariform (*M. simplicifolius* (Fig. 6A,C), *M. elegans*, *M. sp. nov.*, ined. (Lowry 3772), Fig. 6B). Helical thickenings absent.

Vasicentric and vascular tracheids not observed.

Fibres libriform, walls very thick (5-15 µm, up to 20 µm in *M. elegans* and *M. sp. nov.*, ined., Lowry 3772), non-septate and septate (the latter few and located in immediate vicinity of rays in *M. pinnatus* only), with few simple to minutely bordered pits with slit-like apertures primarily in radial walls.

Axial parenchyma apotracheal, rather abundant, diffuse and diffuse-in-aggregates, forming short and longer, occasionally anastomosing tangential lines (Fig. 1A-B, 2A); strands composed of (3-)5-7(-9) cells.

Rays 3-5 per mm, uni- and multiseriate of 2-5 (up to 6 in *M. elegans* and *M. simplicifolius*) cells in width (Fig. 2B). Ray height commonly less than 1 mm. Both multiseriate and uniseriate rays mostly composed of procumbent cells, occasionally with 1-2 marginal rows of square cells (Kribs' Homogenous I, occasionally Heterogeneous III). Pits on tangential walls of ray cells (Fig. 7F-H) mostly rounded and oval, rather large (2-5(-8) µm in diameter). Radial canals present, bordered by thin-walled epithelial cells. Crystals not observed.

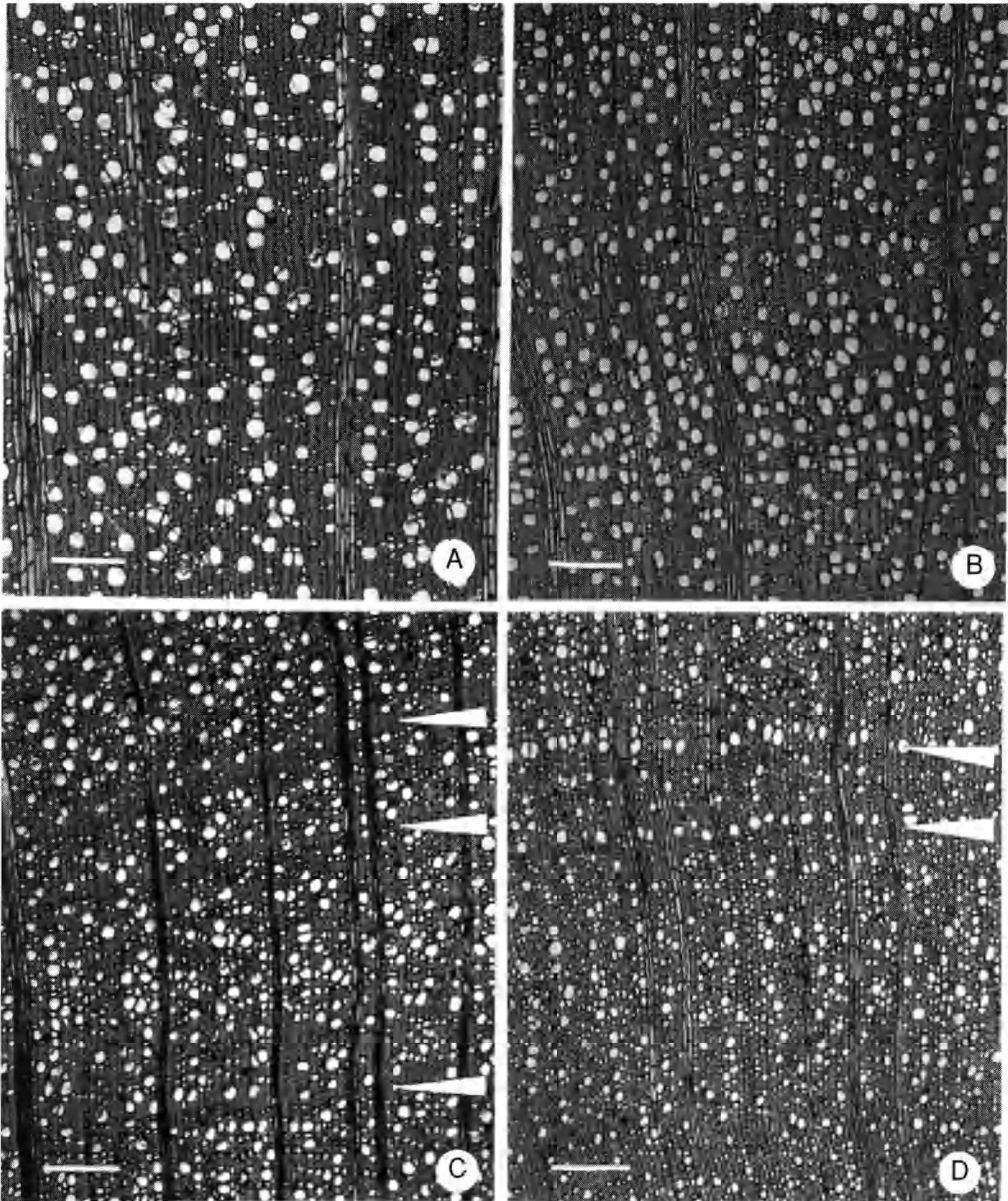


Fig. 1.—Transverse sections: **A**, *Myodocarpus fraxinifolius*, Lowry 3679, growth rings absent.—**B**, *M. simplicifolius*, Lowry 3216, growth rings marked by zones of more numerous vessels and more abundant axial parenchyma tending to form longer tangential rows.—**C**, *Delarbraea harmsii*, Lowry 3685, growth rings marked by zones of scarce axial parenchyma and lower vessel frequency (arrows).—**D**, *Pseudosciadium balansae*, Lowry 3799, growth rings marked by zones of scarce axial parenchyma and by incomplete rows of wider vessels (arrows). Scale bars = 100 μ m.

DELARBREA AND *PSEUDOSCIADIUM* (Fig. 1C-D, 3A-D, 4E-G, 5C,E-G, 6E-G, 7A-E; Table 1).

The wood structure of these genera is very similar, and a combined description is therefore given.

MATERIAL STUDIED.—*Delarbrea harmsii* R. Vig.: New Caledonia, Plateau de Dogny, Lowry 3685; Valley south of Poindimié, Lowry 3909.—*D. michieana* (F. v. Muell.) F. v. Muell.: Australia, Queensland, road from Tully to Mission Beach, Lowry 3626.—*D. montana* Vieill. ex R.Vig. subsp. *arborescens* (Vieill. ex R.Vig.) Lowry: New Caledonia, Mt. Panié, Lowry 3317.—*D. paradoxa* Vieill. subsp. *paradoxa*: New Caledonia, Ile des Pins, Lowry 3750; cult. in St. Petersburg Botanical Garden.—*Pseudosciadium balansae* Baillon: New Caledonia, Mt. Mou, Lowry 3799.

Growth rings absent (*D. harmsii* (Lowry 3909), *D. paradoxa*) or indistinct, marked by zones of

scarce axial parenchyma and lower vessel frequency (*D. harmsii* (Lowry 3685), Fig. 1C), and also by incomplete rows of wider vessels (in the other taxa, Fig. 1D).

Vessels rounded, rarely angular in outline, small (tangential diameter < 70 µm) and numerous (up to 242 per mm² in *D. montana*); solitary with variable portions of radial and tangential multiples of 2-3 (up to 12 in *D. montana*); vessel multiples predominantly tangential in *D. michieana* and *D. montana*. Vessel walls 2-6 µm thick. Tyloses not observed. Vessel elements (310-)540-890(-1300) µm in length. Perforation plates exclusively simple, in more or less oblique end walls (Fig. 4E-G). Intervessel pits alternate, occasionally opposite, 3-6 µm in vertical diameter, rounded, with slit-like apertures surrounded and/or interconnected by shallow, groove-like wall sculptures (Fig. 5C,E-G).

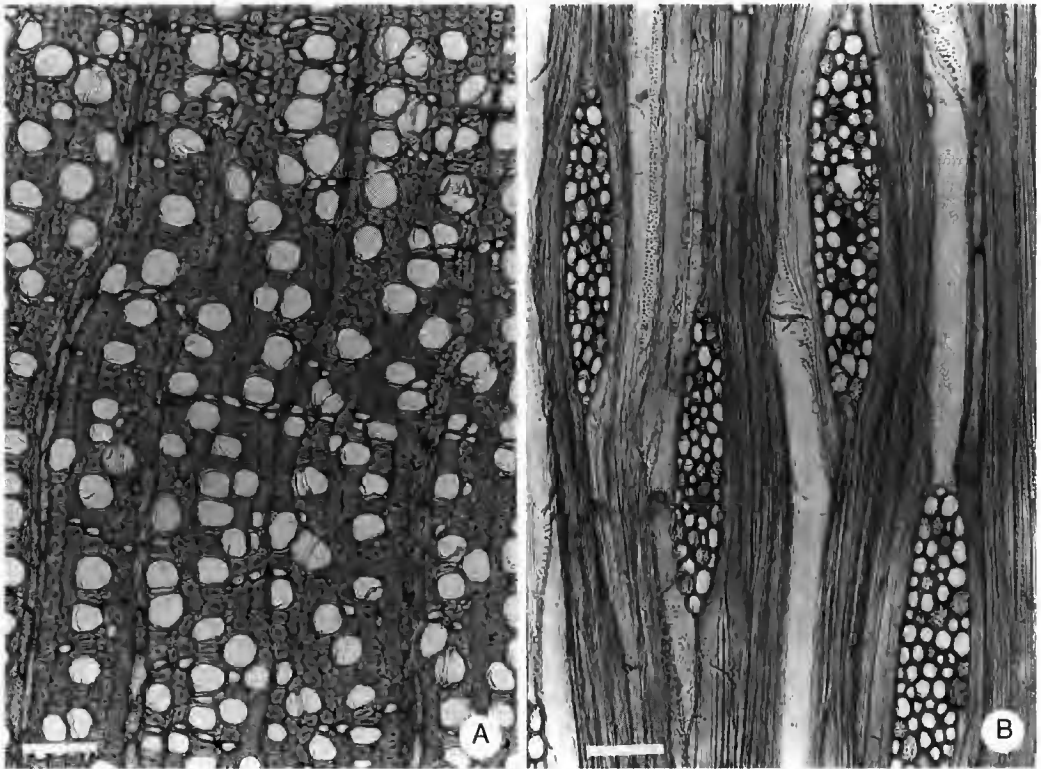


Fig. 2.—A, *Myodocarpus elegans* var. *gracilis*, Lowry 3377A, transverse section: axial parenchyma diffuse-in-aggregates and diffuse, very thick-walled fibers.—B, *M. fraxinifolius*, Lowry 3679, tangential section: multiseriate rays up to 5 rows wide, radial canal. Scale bars = 100 µm.

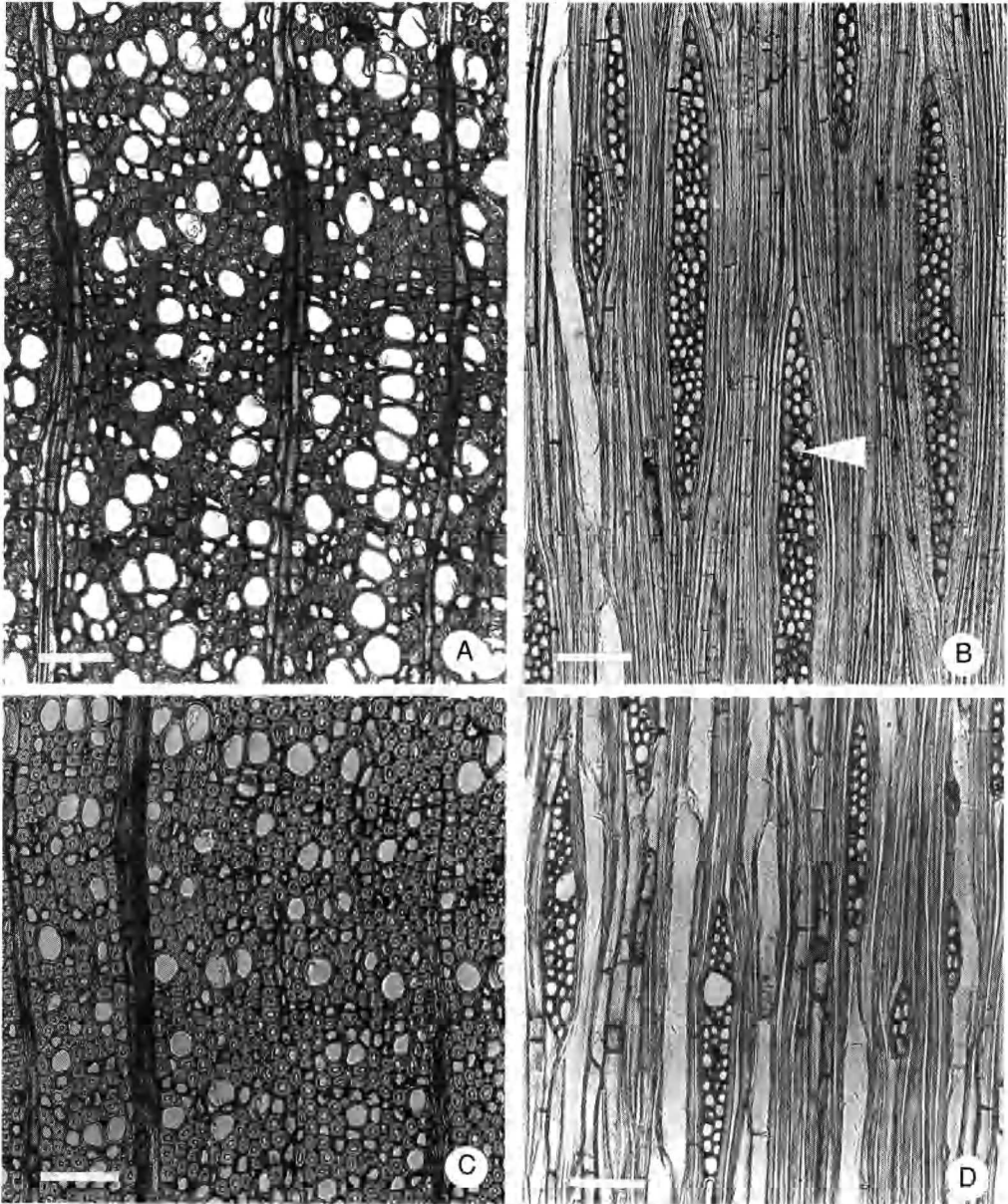


Fig. 3.—A, *Delarbreia harmsii*, Lowry 3685, transverse section: axial parenchyma, diffuse-in-aggregates and diffuse, thick-walled fibers.—B, *D. paradoxa* subsp. *paradoxa*, Lowry 3750, tangential section: multiseriate rays up to 5 rows wide, radial canal (arrow).—C-D, *Pseudosciadium balansae*, Lowry 3799; C, transverse section: parenchyma diffuse-in-aggregates and diffuse, thick-walled fibers; D, tangential section: multiseriate rays up to 3 rows wide, radial canals. Scale bars = 100 μ m.

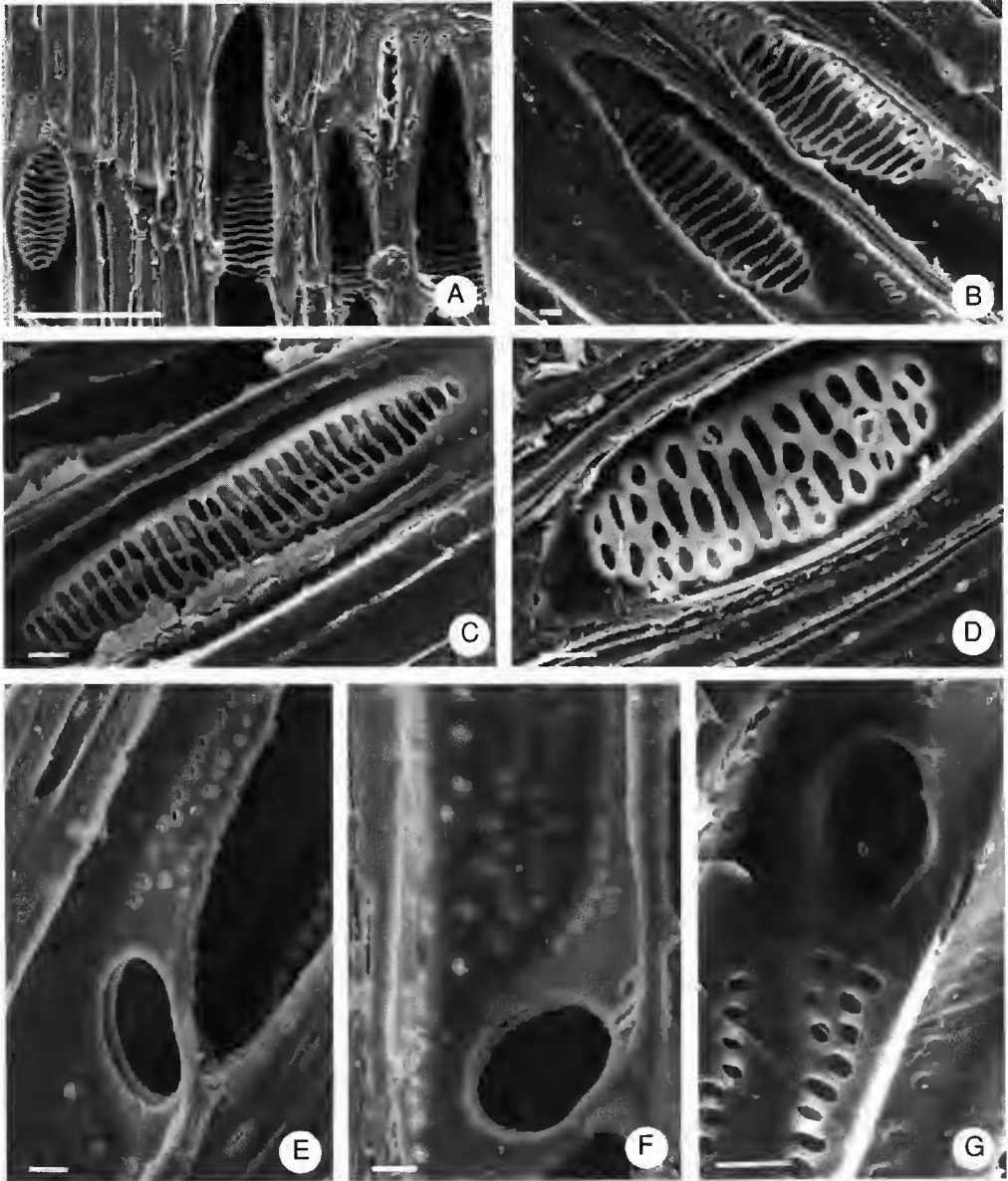


Fig. 4.—Scanning electron micrographs of perforation plates: A-C, perforation plates with numerous bars (A-B, *Myodocarpus simplicifolius*, Lowry 3216; C, *Myodocarpus* sp. nov., ined., Lowry 3772).—D, reticulate perforation plate (*Myodocarpus* sp. nov., ined., Lowry 3772).—E-G, simple perforation plates (E, *Delarbrea harmslii*, Lowry 3685; F, *D. paradoxa* subsp. *paradoxa*, Lowry 3750; G, *Pseudosciadium balansae*, Lowry 3799). Scale bar of A = 100 μ m; of B-G = 10 μ m.

Vessel-ray pits similar to intervessel pits in size and shape (Fig. 6E-G). Helical thickenings found only in one sample of *D. harmsii* (Lowry 3909, Fig. 5F, 6F), but absent in others (including the second sample of *D. harmsii* studied, Lowry 3685, Fig. 5G, 6E).

Vasicentric tracheids rather numerous in *D. paradoxa* subsp. *paradoxa* but absent in the other species.

Fibres libriform, thick-walled (4-10 μm , up to

16 μm in *D. harmsii*), non-septate (occasionally septate in *D. paradoxa*), with small to rather large (> 3 μm) bordered pits in both radial and tangential walls.

Axial parenchyma apotracheal diffuse and diffuse-in-aggregates, rather abundant, often forming anastomosing, discontinuous tangential lines (Fig. 1C-D, 3A,C), strands composed of (2-)3-5(-7) cells.

Rays 2-5 per mm, mostly multiseriate of 2-3

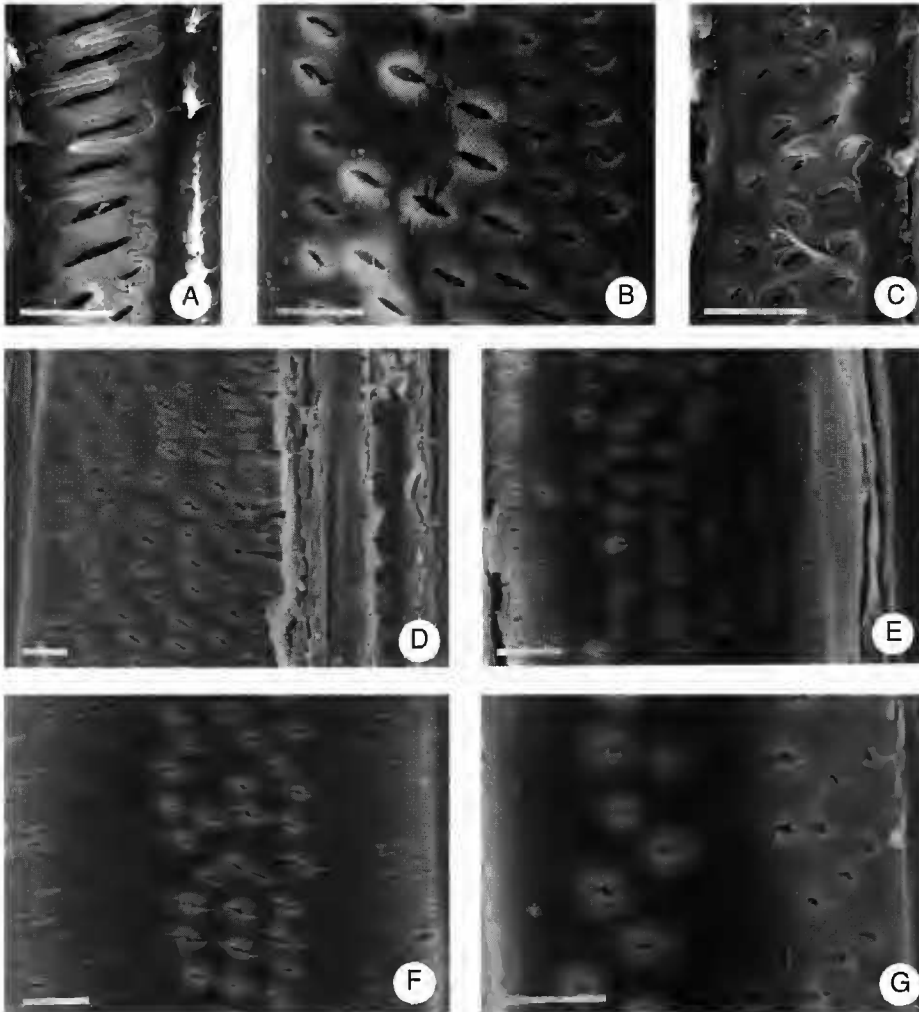


Fig. 5.—Scanning electron micrographs of intervessel pitting: A, scalariform pitting (*Myodocarpus* sp. nov., ined., Lowry 3772).—B-G, alternate pitting composed of pits with slit-like apertures surrounded and/or interconnected by shallow, groove-like wall sculptures (B, *M. pinnatus*, Lowry 3318; C, *Pseudosciadium balansae*, Lowry 3799; D, *M. simplicifolius*, USw W-4736; E, *Delarbrea paradoxa* subsp. *paradoxa*, Lowry 3750; F, *D. harmsii*, Lowry 3909, note helical thickenings on the vessel wall; G, *D. harmsii*, Lowry 3685, note absence of helical thickenings). Scale bars = 10 μm .

(up to 5 in *D. montana*, and to 6 in *D. paradoxa*) cells in width (Fig. 3B,D); uniseriate rays scanty in *Delarbrea* (except *D. michieana*), more numerous in *Pseudosciadium*; in *D. michieana* rays considerably more numerous (9-10 per mm)

than in others. Both multiseriate and uniseriate rays composed of procumbent cells, occasionally with 1-2 marginal rows of square cells (Kribs' Homogenous I, occasionally Heterogeneous III). Pits on the tangential walls of ray cells (Fig. 7A-E)

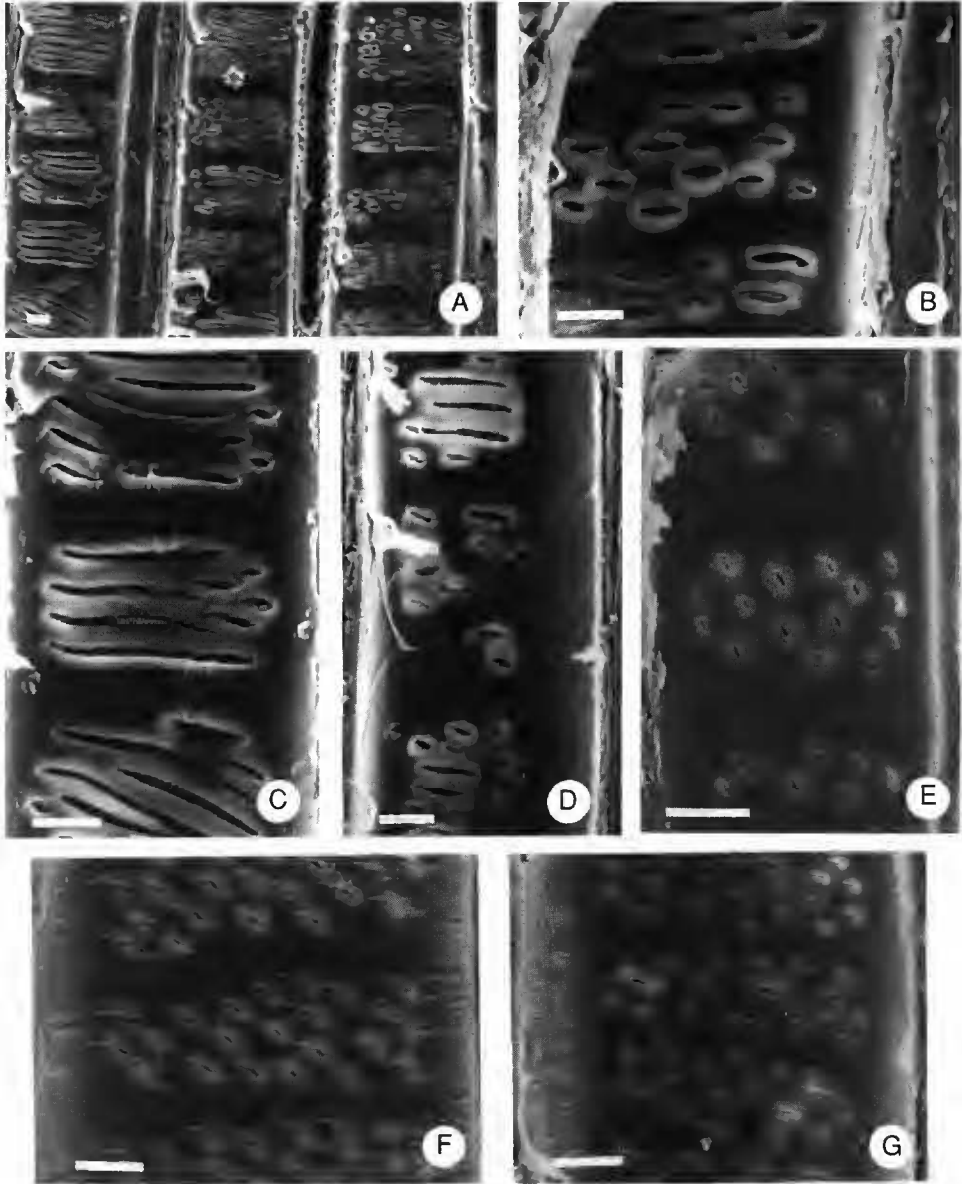


Fig. 6.—Scanning electron micrographs of vessel-ray pitting: **A, C-D**, vessel-ray pitting composed of both scalariform and rounded or oval pits (**A, C**, *Myodocarpus simplicifolius*, Lowry 3216; **D**, *Myodocarpus* sp. nov., ined, Lowry 3772).—**B, E-G**, vessel-ray pitting composed of rounded and oval pits only (**B**, *M. pinnatus*, Lowry 3318; **E**, *Delarbrea harmsii*, Lowry 3685, note absence of helical thickenings; **F**, *D. harmsii*, Lowry 3909, note helical thickenings on the vessel wall; **G**, *D. paradoxa* subsp. *paradoxa*, Lowry 3750). Scale bars = 10 µm.

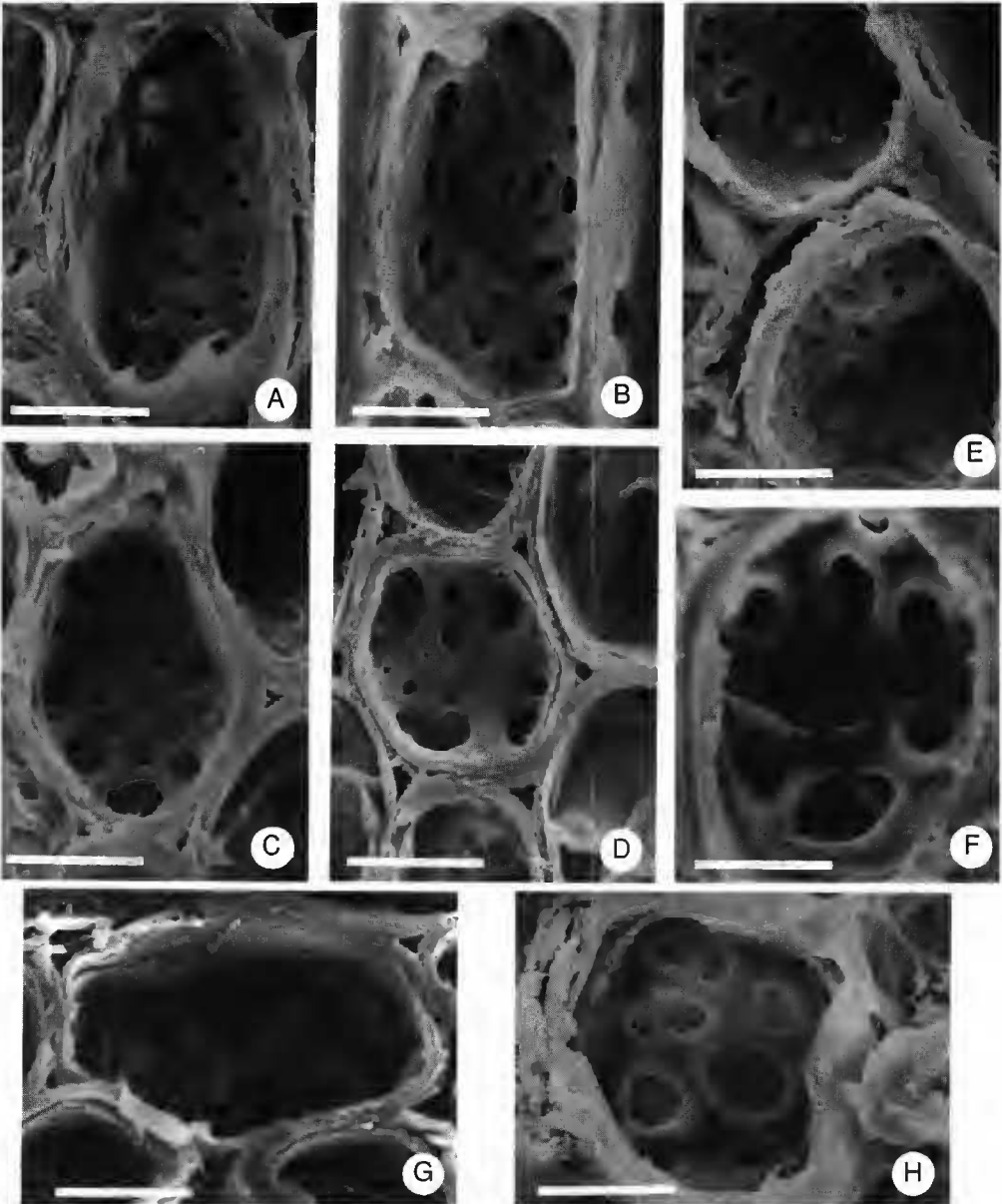


Fig. 7.—Scanning electron micrographs of tangential walls of ray cells: A-E, relatively small pits (A, *Delarbrea montana* subsp. *arborea*, Lowry 3317; B-C, *D. harmsii*, Lowry 3909; D, *D. harmsii*, Lowry 3685; E, *Pseudosciadium balansae*, Lowry 3799).—F-H, larger pits (F, *Myodocarpus simplicifolius*, Lowry 3216; G, *M. pinnatus*, Lowry 3318; H, *M. simplicifolius*, USW W-4736). Scale bars = 10 μ m.

rounded, oval, elongate, 1-3 µm in diameter (up to 5 µm in *D. harmsii* and *D. paradoxa*). Radial canals present, bordered by thin-walled epithelial cells. Crystals not observed.

DISCUSSION

These results strongly support the idea (LOWRY 1986a, 1986b) that *Myodocarpus*, *Delarbrea* (including *D. michieana* originally described as a separate genus *Pornspermum*), and *Pseudosciadium* form a closely related monophyletic group. This alliance differs sharply from other Araliaceae by the presence of apotracheal (diffuse and diffuse-in-agregates) axial parenchyma. Moreover, members of the genera studied have several other wood characters that are unusual for Araliaceae, including small intervessel pits (3-6 µm), exclusively thick- to very thick-walled

libriform fibres, and large bordered fibre pits (the last feature occurs in *Delarbrea* and *Pseudosciadium* only). These data do not support BAUMANN's (1946) view that *Myodocarpus* is a link between Araliaceae and Apiaceae, since apotracheal axial parenchyma of this type has not been found in either family except in the three taxa studied here (METCALFE & CHALK 1950; RODRIGUEZ 1957, 1971; OSKOLSKI & LOWRY in prep.). As for other plant groups usually regarded as possible relatives of Araliales, the wood features of *Myodocarpus*, *Delarbrea*, and *Pseudosciadium* are in some respects similar to those found in certain Cornalean families (Cornaceae *sensu lato*, Alangiaceae) based on the presence of the axial parenchyma type, and also the occurrence of large bordered fibre pits. However, the genera studied here differ markedly from the latter by their predominantly homogeneous rays and by the presence of radial canals (ADAMS 1949;

TABLE 1.—Wood anatomical features of taxa studied.

Taxon (voucher collection number)	Character									
	1	2	3	4	5	6	7	8	9	10
<i>Myodocarpus fraxinifolius</i> (Lowry 3679)	35	1239	57	41/7	101	10/0-18	1580	5	0.4	2.5
<i>M. fraxinifolius</i> (USW 20844)	50	1050	52	51/5	75	8/5-14	1376	5	1.0	3.2
<i>M. elegans</i> var. <i>gracilis</i> (Lowry 3377)	16	1160	33	34/7	282	8/6-20	1093	6	2.8	2.5
<i>M. sp. nov.</i> ined. (Lowry 3771)	15	832	41	62/5	138	14/7-18	1159	4	2.3	2.3
<i>M. pinnatus</i> (Lowry 3318)	25	995	61	40/5	93	9/5-15	1398	5	2.2	3.1
<i>M. simplicifolius</i> (Lowry 3216)	22	1042	46	52/5	157	10/8-20	1555	6	2.6	2.2
<i>M. simplicifolius</i> (USW W-4736)	50	1132	54	49/5	108	15/8-29	1343	6	1.9	2.9
<i>Delarbrea harmsii</i> (Lowry 3685)	45	870	47	54/4	114	0	1320	3	0.4	3.2
<i>D. harmsii</i> (Lowry 3909)	50	890	55	50/4	100	0	1423	3	0.2	3.8
<i>D. michieana</i> (Lowry 3626)	15	638	34	40/5	217	0	857	3	2.5	7.0
<i>D. montana</i> subsp. <i>arborea</i> (Lowry 3317)	10	789	32	28/12	242	0	1079	5	0.3	3.4
<i>D. paradoxa</i> subsp. <i>paradoxa</i> (Lowry 3750)	30	573	49	58/5	89	0	1093	6	0.4	3.8
<i>D. paradoxa</i> subsp. <i>paradoxa</i> (cult. in SPb Bot. Gard.)	10	540	46	56/4	157	0	814	5	1.6	4.4
<i>Pseudosciadium balansae</i> (Lowry 3799)	25	640	32	61/4	119	0	1080	3	1.0	2.5

1: Radius of wood sample (mm).—2: Average length of vessel elements (µm).—3: Average tangential diameter of vessels (µm).—4: Percentage of solitary vessels / the greatest number of vessels in a vessel group.—5: Vessel and vasicentric tracheid frequency (per sq. mm).—6: Usual / min.-max. number of bars per perforation plate.—7: Average length of libriform fibres (µm).—8: Width of multiseriate rays (maximum, cells).—9: Number of uniseriate rays per mm.—10: Number of multiseriate rays per mm.

METCALFE & CHALK 1950; LI & CHAO 1954). The results provided here are consistent with the data presented in a recent study (OSKOLSKI 1994) based on more limited material.

The wood anatomy of *Pseudosciadium* does not deviate substantially from that of *Delarbreia*. Hence, data on wood structure are consistent with LOWRY'S (1986a, 1986b) view that *Pseudosciadium* is closely related to both *Delarbreia* and *Myodocarpus*, rather than being allied to *Mackinlaya* (including *Anomopanax*; PHILIPSON 1951, 1979) and *Apiopetalum* as suggested by several earlier authors (HARMS 1894-1897; VIGUIER 1906, 1925; HUTCHINSON 1967). However, because no data on the wood anatomy of *Mackinlaya* or *Apiopetalum* are currently available, it is not possible to make any comparison on the basis of wood features. Although the wood of "*Anomopanax cumingianus*" (K. Presl) Merrill was studied by RODRIGUEZ (1957), this species in fact belongs in the genus *Polyscias* (*P. cumingiana* (K. Presl) Fern.-Vill.).

The wood of *Myodocarpus* differs from that of *Delarbreia* and *Pseudosciadium* by its somewhat longer vessel elements (Table 1), almost exclusively scalariform perforations, thicker-walled fibres, absence of large bordered fibre pits, and larger pits between ray cells. Although the large bordered fibre pits that occur in *Delarbreia* and *Pseudosciadium* are generally regarded as primitive, when the full set of features examined is taken into consideration, the wood structure of *Myodocarpus* is distinctly more primitive (sensu BAILEY) than that of the other two genera. In addition to differences in the vessel element morphology; the more primitive nature of *Myodocarpus* wood is indicated by the type of intervessel and vessel-ray pitting; scalariform, transitional, and alternate pitting is found in *Myodocarpus*, while in *Delarbreia* and *Pseudosciadium* only alternate to occasionally opposite pitting has been observed.

The size and shape of the pits on the tangential walls of adjacent ray cells are also of important diagnostic value within the taxa studied. *Myodocarpus* (Fig. 7F-H) differs from both *Delarbreia* (Fig. 7A-D) and *Pseudosciadium* (Fig. 7E) by the large size of these pits. The fine

structure of ray and axial parenchyma cell walls has been very useful as a diagnostic character at the generic and infrageneric level for gymnosperms (CHAVCHAVADZE 1979), but has been used for this purpose only rarely in angiosperms (e.g., FUJII et al. 1994). It would be interesting to assess the diagnostic value of these characters within a range of flowering plants, and such a study would be facilitated by the fact that these features are easily observed by SEM.

While the wood anatomy of the *Myodocarpus* species examined is rather uniform, two groups can tentatively be distinguished based on the shape of their intervessel and vessel-ray pits. Group 1, which includes *M. pinnatus* and *M. fraxinifolius*, has only oval and rounded vessel-ray and intervessel pits. Group 2, comprising *M. simplicifolius*, *M. elegans*, and *M. sp. nov.*, ined. (Lowry 3772), has scalariform as well as oval and rounded vessel-ray pits, and its intervessel pits are occasionally also scalariform. The delimitation of these two groups is consistent with a fundamental difference in leaf morphology: the two members of Group 1 have pinnately compound leaves, while the Group 2 species (and indeed all other species of *Myodocarpus*) have exclusively simple leaves.

The qualitative wood structural features of the species of *Delarbreia* and *Pseudosciadium* examined are also uniform, including the shape of the intervessel and vessel-ray pits. Based on the limited sample studied here, two species groups can, however, be tentatively distinguished within this alliance: *D. harmsii*, *D. michiana*, and *P. balansae*, with rays up to 3 cells wide; and *D. montana* subsp. *arborea* and *D. paradoxa* subsp. *paradoxa*, with rays up to 5-6 cells wide. The inter-ray pits of *D. paradoxa* and *D. harmsii* are slightly larger than in *D. montana* subsp. *arborea* and *Pseudosciadium balansae*, but this is considered a less reliable basis for discriminating species groups. It would be useful to examine these features in a larger set of samples of these taxa.

The presence of vasicentric tracheids was recently considered by the first author (OSKOLSKI 1994, 1996) as a generic character of *Delarbreia*, based on the study of a single sample of *Delarbreia paradoxa* subsp. *paradoxa*. While a second sample of this taxon also possesses vasi-

centric tracheids, all other species of *Delarbreia* examined to date lack this feature. Moreover, although OSKOLSKI (1994, 1996) made no distinction between vascular and vasicentric tracheids in *D. paradoxa* subsp. *paradoxa*, they should be referred to the second type because of the absence of the growth rings in this taxon, whereas vascular tracheids are always associated with latewood vessel clusters in species that exhibit growth rings (I.A.W.A. Committee, 1989).

CARLQUIST (1985, 1988) considers vasicentric tracheids as an adaptation to ensure adequate water conduction in conditions of extreme water stress. This idea suggests a hypothesis to explain the adaptive importance of the vasicentric tracheids in *D. paradoxa* subsp. *paradoxa*, which is most common and wide-ranging member of the genus, and indeed of any Araliaceae in the Malesian region (LOWRY 1986a, 1986b, 1989), with at least some populations occurring in areas that periodically undergo dry conditions. It would be interesting to analyze a larger sample of *D. paradoxa* subsp. *paradoxa*, and also to determine whether vasicentric tracheids occur in *D. paradoxa* subsp. *depauperata*, whose distribution is restricted to northeastern New Caledonia, the driest part of the island.

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REFERENCES

- ADAMS J.E. 1949.—Studies in the comparative anatomy of the Cornaceae. *J. Elisha Mitchel Sci. Soc.* 65: 218-244.
- BAUMANN M.G. 1946.—*Myodocarpus* und die Phylogenie der Umbelliferen-Früchte. *Ber. Schweiz. Bot. Ges.* 56: 13-112.
- BAILLON H. 1878.—Recherches nouvelles sur les Araliées et sur la famille Umbellifères en général. *Adansonia* 12: 125-178.
- BAILLON H. 1879.—Ombellifères. *Hist. Pl.* 7: 66-256.
- BENTHAM G. 1867.—Araliaceae: 931-947, in G. BENTHAM & J.D. HOOKER, *Genera plantarum*. 1. A. Black, W. Pamplin, Lovell Reeve & Co., Williams & Norgate, London.
- CARLQUIST S. 1985.—Vasicentric tracheids as a drought survival mechanism in the woody flora of southern California and similar regions; review of vasicentric tracheids. *Aliso* 11: 37-68.
- CARLQUIST S. 1988.—*Comparative wood anatomy*. Springer Verlag, Berlin.
- CHAVCHAVADZE E.S. 1979.—*Anatomy of the Coniferous woods*. Nauka, Leningrad (In Russian).
- EXLEY R.R., MEYLAN B.A. & BUTTERFIELD B.G. 1977.—A technique for obtaining clear cut surfaces on wood samples prepared for the scanning electron microscope. *J. Microscopy* 110: 75-78.
- EYDE R.H. & TSENG C.C. 1971.—What is the primitive floral structure of Araliaceae? *J. Arnold Arbor.* 52: 205-239.
- FUJII T., BAAS P., GASSON P. & RIDDER-NUMAN J.W.A. 1994.—Wood anatomy of the *Sophora* Group (Leguminosae): 205-249, in I.K. FERGUSON & S.C. TUCKER (eds.), *Advances in Legume Systematics*, vol. 6. Royal Botanic Gardens, Kew.
- HARMS H. 1894-1897.—Araliaceae: 205-249, in A. ENGLER & K. PRANTL (eds.), *Die natürlichen Pflanzenfamilien* III, 8. W. Engelmann, Leipzig.
- HUTCHINSON J. 1967.—Araliaceae. *The Genera of Flowering Plants* 2: 52-81. Oxford Univ. Press, London.
- I.A.W.A. Committee 1989.—I.A.W.A. list of microscopic features for hardwood identification. *I.A.W.A. Bull.*, N. S., 10: 219-332.
- KRIBS D.A. 1937.—Salient lines of structural specialization in the wood parenchyma of dicotyledons. *Bull. Torrey Bot. Club* 64: 177-186.
- LI H.L. & CHAO C.Y. 1954.—Comparative anatomy of the woods of the Cornaceae and allies. *Quart. J.*

- Taiwan Mus.* 7: 119-136.
- LOWRY P.P. II. 1986a.—A systematic study of three genera of Araliaceae endemic to or centered on New Caledonia: *Delarbrea*, *Myodocarpus*, and *Pseudosciadium*. Ph.D. Thesis, Washington Univ., St. Louis.
- LOWRY P.P. II. 1986b.—A systematic study of *Delarbrea* Vieill. (Araliaceae). *Allertonia* 4: 169-201.
- LOWRY P.P. II. 1987.—A synopsis of native Hawaiian Araliaceae. *Pacific Sci.* 40: 79-87.
- LOWRY P.P. II. 1988.—Notes on the Fijian endemic *Meryta tenuifolia* (Araliaceae). *Ann. Missouri Bot. Gard.* 75: 389-391.
- LOWRY P.P. II. 1989.—A revision of Araliaceae from Vanuatu. *Bull. Mus. Natl. Hist. Nat., B, Adansonia* 11: 117-155.
- LOWRY P.P. II. 1990.—Araliaceae: 224-237, in W.L. WAGNER, D.L. HERBST & S.H. SOHMER (eds.), *Manual of the flowering plants of Hawaii*, vol. 1. Univ. Hawaii Press, Bishop Museum Press, Honolulu.
- LOWRY P.P. II. (in press).—Diversity, endemism, and extinction in the flora of New Caledonia: a review. *Proc. Intl. Symposium on Rare, Threatened, and Endangered Floras of Asia and the Pacific* Academia Sinica, Taipei, Taiwan.
- LOWRY P.P. II., MILLER J.S. & FRODIN D.G. 1989.—New combinations and name changes for some cultivated tropical Old World and Pacific Araliaceae. *Baileya* 23: 5-13.
- METCALFE C.R. & CHALK I. 1950.—*Anatomy of the dicoryledons*, vol. 2. Clarendon Press, Oxford.
- MEYLAND B.A. & BUTTERFIELD B.C. 1978.—*The structure of New Zealand woods*. N. Z. DSIR, Wellington.
- OSKOLSKI A.A. 1994.—*Wood anatomy of Araliaceae*. Komarov Bot. Institute., St. Petersburg (In Russian).
- OSKOLSKI A.A. 1995.—Wood anatomy of *Schefflera* and related taxa (Araliaceae). *I.A.W.A. J.* 16: 191-215.
- OSKOLSKI A.A. 1996.—A survey of the wood anatomy of the Araliaceae: 99-119, in L.A. DONALDSON, A.P. SINGH, B.G. BUTTERFIELD & L.J. WHITEHOUSE (eds.), *Recent Advances in Wood Anatomy*. N. Z. Forest Res. Inst.
- PHILIPSON W.R. 1951.—Contributions to our knowledge of Old World Araliaceae. *Bull. British Mus. Nat. Hist., Bot.* 1: 3-20.
- PHILIPSON W.R. 1979.—Araliaceae, part 1. *Flora Malesiana*, Ser. 1, 9: 1-105.
- PLUNKETT G.M. 1994.—A molecular-phylogenetic approach to the "family-pair dilemma" in Apiales and Cyperales. Ph.D. Thesis, Washington State Univ., Pullman.
- PLUNKETT G.M., SOLTIS D.E. & SOLTIS P.S. 1996.—Higher level relationships of Apiales (Apiaceae and Araliaceae) based on phylogenetic analysis of *rbcL* sequences. *Amer. J. Bot.* 83: 499-515.
- RAVEN P.H. 1980.—Plate tectonics and southern hemisphere biogeography: 3-24, in K. LARSEN & L.B. HOLM-NIELSEN (eds.), *Tropical botany*. Academic Press, London, New York & San Francisco.
- RAVEN P.H. & AXELROD D.I. 1972.—Plate tectonics and Australasian paleobiogeography. *Science* 176: 1379-1386.
- RAVEN P.H. & AXELROD D.I. 1974.—Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539-673.
- RECORD S.J. & HESS R.W. 1944.—*Timbers of the New World*. Yale School of Forestry, New Haven.
- RODRIGUEZ R.L. 1957.—Systematic anatomical studies on *Myrrhidendron* and other woody Umbellales. *Univ. Calif. Publ. Bot.* 29: 145-318.
- RODRIGUEZ R.L. 1971.—The relationships of the Umbellales: 63-91, in V.H. HEYWOOD (ed.), *The Biology and Chemistry of the Umbelliferae*. Bot. J. Linn. Soc., Suppl. 1, 64. Academic Press, London & New York.
- SARLIN P. 1954.—*Bois et forêts de la Nouvelle-Calédonie*. Centre Tech. For. Trop., Nogent-sur-Marne.
- TAKHTAJAN A.L. 1987.—*Systema Magnoliophytorum*. Nauka, Leningrad (In Russian).
- THORNE R.F. 1973.—Inclusion of the Apiaceae (Umbelliferae) in the Araliaceae. *Notes Roy. Bot. Gard. Edinburgh* 32: 161-165.
- TSENG C. & HOO C. 1982.—A new classification scheme for the family Araliaceae. *Acta Phytotax. Sinica* 20: 125-129.
- VIEILLARD E. 1865.—Plantes de la Nouvelle-Calédonie recueillies par M. Eugène Vieillard, Chirurgien de la Marine. *Bull. Soc. Linn. Normandie* 9: 332-348.
- VIGUIER R. 1906.—Recherches anatomiques sur la classification des Araliacées. *Ann. Sci. Nat. Bot.*, sér. 9, 4: 1-210.
- VIGUIER R. (1910-1913) 1925.—Contribution à l'étude de la flore de Nouvelle-Calédonie: Araliacées. *J. Bot. (Morot)*, sér. 2, 3: 38-101.

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